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Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff National Park, Canada

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Abstract

The effects of prescribed burning on forage abundance and suitability for elk (*Cervus elaphus*) during the snow-free season was evaluated in east-central Banff National Park, Canada. Six coniferous forest and mixed shrub–herb plant communities ($n=144$ plots), and 5223 ha of burned ($n=131$) vegetation <12 years old were sampled using a stratified semi-random design. Sampling units represented various combinations of vegetation, terrain conditions, and stand ages that were derived from digital biophysical data, with plant communities the basic unit of analysis. Burning coniferous forest stands reduced woody biomass, and increased herbaceous forage from 146 to 790 kg/ha. Increases commonly occurred in the percent cover of hairy wild rye (*Leymus innovatus* (Beal) Pigler) and fireweed (*Chamerion angustifolium* (L.) Holub.). The herbaceous components of mixed shrub–herb communities increased from 336–747 kg/ha to 517–1104 kg/ha in response to burning ($P<0.025$, Mann–Whitney *U*-test). Browse biomass (mostly *Salix* spp. and *Betula nana* L.) increased ≥220% ($P\leq0.003$, Mann–Whitney *U*-test) from 653 kg/ha in deciduous shrub types. Elk preferences for unburned and burned vegetation-types were assessed as low and moderate, respectively. Potential summer carrying capacity, based on forage availability, increased from eight to 28 elk/100 km^2 within burned areas, whereas spring grazing potential rose from 13 to 45 elk/100 km^2. Most of the increase (73%) was attributable to changes within burned Engelmann Spruce stands, which composed 58% of the burned area.

Keywords: Biomass; *Cervus elaphus*; Rocky mountains; Vegetation

1. Introduction

For at least 300 years before European settlement during the early 20th century, valley-bottom and lower Subalpine slopes of the central Canadian Rocky Mountains in southwest Alberta experienced historic fire return intervals ranging from 65 to 150 years (Tande, 1979; Johnson and Fryer, 1987). In contrast, higher elevation Subalpine areas tended to experience cycles of 150–300 years (Arno, 1980; Hawkes, 1979). Lightning strikes can be an important natural ignition source on the western slopes of the Rocky Mountains, however, they are too rare to explain fire frequencies immediately east of the Continental Divide (Kay et al., 1999; Wierzchowski et al., 2002). There is historical and archaeological evidence suggesting aboriginals used fire along valley-bottoms to maintain grassy areas, possibly as wildlife habitat (Lewis, 1989; Barrett and Arno, 1982; Gruell, 1985; White et al., 2001a,b). Whether lightning or human-caused, the role of historic fire regimes in defining the composition of the natural landscape has been the subject of considerable debate in western Canada, especially within the national parks system (e.g. Kay et al., 1999; Wierzchowski et al., 2002).

Fire suppression in Banff National Park became a priority about 1909 and has been effectively applied (White, 1985; Kay et al., 1999, pp. 5–25). Consequently, fire exclusion resulted in encroachment by lodgepole pine (*Pinus contorta* Dougl. *ex* Loud.) into lower valley areas, where some of the best quality elk (*Cervus elaphus*) foraging areas exist (Holroyd and Van Tighem, 1983).

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This has also resulted in increased homogeneity in vegetation composition, age, and structure; and many mature and over-mature coniferous forests. According to Parks Canada policy, an important role of national park managers is to maintain natural disturbance regimes (Heritage Canada, 1994, pp. 33–34). Managers of Banff National Park have accepted 50-, 100-, and 300-years, depending upon climatic zone, as the historic fire return intervals (Banff National Park, 1995; White et al., 2003; Rogeau et al., 2004). Because lightning-caused wildfires are rare within the park (Kay et al., 1999, pp. 4–5), prescribed burning is employed to increase the spatial extent of fire affected lands up to 50% of the historic average (Banff National Park, 1997). Full restoration of the fire regime was not considered desirable due to the encroachment of development and the proximity of commercial forests and private land ownership immediately east of the park (Wierzchowski, 1995). Priorities of the prescribed burning program of Banff National Park (1997) include revitalizing decadent and declining forests, controlling lodgepole pine encroachment on sites once dominated by grass and shrub vegetation, and improving habitat quality for wildlife species such as elk.

The purposes of this study were to (i) evaluate elk forage suitability during the snow-free season within unburned and recently burned plant communities in the east-central portion of Banff National Park, and (ii) to determine the degree of elk habitat enhancement achieved through prescribed burning.

2. Study area

The study was conducted along the eastern slopes of the Rocky Mountains, primarily within the Eastern Slopes Ecological Management area of Banff National Park in Alberta, Canada (Fig. 1). The study area consists of about 1285 km^2 of mountainous terrain, with elevations ranging from 1650 to 3300 m. Included within this area are headwater tributaries of the Clearwater and Red Deer rivers. Three major valleys in the area are narrow and run primarily in a west–east direction. Subalpine and Alpine ecoclimatic zones dominate the study area (Holland and Coen, 1982), but minor areas of Upper Boreal-Cordilleran and Montane vegetation do occur in lower valley positions at the eastern edge (Stelfox, 1981; Rayner, 1984; Strong, 1992). The Subalpine zone can be divided into lower and upper subzones. The lower subzone is primarily vegetated by lodgepole pine, with Engelmann spruce (*Picea engelmannii* Parry *ex* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) being secondary successional species. Mixed grass and shrub vegetation is scattered throughout the area in valley bottoms and on steep south-facing slopes. The upper subzone is dominated by Engelmann spruce and subalpine fir, which favor moist soils and the lower fire frequency sites associated with higher elevations. Meadows and stunted trees form the upper limit of this zone. The Subalpine and Alpine zones interface at about 2100 m (Stelfox, 1981; Rayner, 1984). The Alpine zone occurs in the highest elevations, and consequently the coldest temperatures and greatest precipitation. Meadows are the most common vegetation, but about 43% of the Alpine zone is unvegetated.

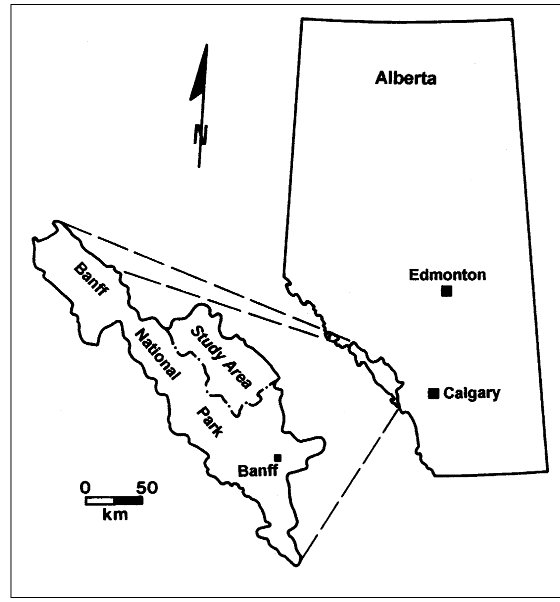

Fig. 1. Location of the study area within east-central banff national park, Alberta.

In photographs recorded in 1915, grass-and shrub-dominated valleys and lower slopes characterized the area, whereas trees colonized upper slopes. This pattern contrasts with the dominance of coniferous forests today (Kay et al., 1999, pp. 4–26; Rhemtulla et al., 2002). It is believed that the change is the result of fire suppression (Rhemtulla et al., 2002; White et al., 2001b). In the 20th century, 46 km^2 of vegetated land burned within the study area compared to at least 120 km^2 in the 19th century (Rogeau and Rogeau, 1994). Between September 1989 and June 1999, Banff National Park staff intentionally burned an additional 52 km^2 of land within the study area (White et al., 2003).

Rocky Mountain elk inhabit the foothills and mountainous areas of Alberta and British Columbia. They are highly opportunistic and adapted to many ecological conditions (Geist, 2002). In the eastern slopes of Banff National Park, they use Montane, Subalpine, and Alpine environments, depending on season, plant phenology, and snow depths (Morgantini and Hudson, 1988). They use meadows and shrublands for foraging, whereas forests provide hiding and thermal cover (Skovlin et al., 2002; McCorquodale, 1991; Peck and Peek, 1991). Optimal forage:cover ratios for elk vary from 40:60 to 60:40 (Skovlin et al., 2002; Thomas et al., 1979). There are about 1000 elk in the area (Morgantini and Hudson, 1989).

3. Methods

3.1. Field sampling

Prior to field sampling, the study area was stratified on a pixel basis (30-m×30-m image resolution) according to vegetation and terrain conditions using ArcView (Environmental Systems Research Institute, 1999). Landscape stratification was based on an existing vegetation classification (Wierzchowski, 2000), with prescribed burning, forest stand age, slope orientation, elevation, and percent slope data provided by Banff National Park. Prescribed burn areas were further classified as 2–3 years or 7–11 years old, which corresponded with the two main periods of prescribed burning (1998–1999 and 1989–1994). Pixels with $>30°$ slopes were excluded from the analysis, because elk do not typically forage on steeper slopes (Hershey and Leege, 1982; Skovlin et al., 2002). Excluded from the analysis were also sites less than 60-m×60-m in size and areas above 2000 m in elevation; the latter because no prescribed burning occurred within the Alpine zone.

Potential sampling sites were arbitrarily selected from the pool of available vegetation-terrain units. An attempt was made to evenly distribute the number of samples among all strata, subject to the availability of sites and reasonable accessibility. A sampling point was arbitrarily picked within each vegetation-terrain unit, and located in the field with a hand-held global positioning system unit. Some sites were not sampled due to vegetation misclassification, but alternative sites were sampled near the intended location.

Pre-selected sampling coordinates also served as the transect starting point. Transects on slopes were placed perpendicular to the gradient with the orientation determined by a coin flip. A randomly selected number corresponding to a cardinal direction was used to orient transects on flat or irregular terrain. Vegetation <1 m tall was sampled within 1.5-m×1.5-m quadrats located at the 7.5-, 15-, and 22.5-m marks along a 30-m tape. This amount of quadrat area (6.75 m^2) equaled or exceeded the quantities associated with other comparable studies (e.g. 4 m^2-Mueggler and Stewart, 1980; 5 m^2-Cooper et al., 1987; 1 m^2-Willoughby et al., 2004). Quadrats were located on the upslope side of the transect to facilitate viewing and to minimize trampling. Within each quadrat, percent cover was ocularly estimated to the nearest percent for growth-forms and individual species. Species with $<1\%$ cover were not included. A 5-m wide strip on each side of the transect (i.e. a 10-m×30-m plot) was used to estimate the cover of trees and shrubs >1 m tall, which meets the minimal areal limits suggested by Mueller-Dombois and Mueller-Dombois and Ellenberg (1974), p. 48). Tree canopy cover was measured using a densiometer at each 1.5-m×1.5-m quadrat. A 20-cm×50-cm frame was placed in the center of the two terminal quadrats and clipped. Herbaceous plants were cut as close to the ground as possible, and the current annual growth of twigs with leaves for woody plants within the browsing zone (<2 m) were clipped. Clipped samples were air-dried in the field and then weighed. Plant nomenclature was based on Kartesz and Wilson (1998).

The density of trees in individual forest stands was determined based on measures at the 7.5-, 15-, and 22.5-m marks along the sampling tape, using the point-centered quarter method (Mueller-Dombois and Ellenberg, 1974, p. 110). The southern-most tree at each sampling station was used for tree height and diameter at breast height (1.3 m) measurements. Percent slope, slope orientation and position (e.g. toe, middle slope, crest), and elevation were determined for each site. Only the current year's spring and summer elk pellet groups were counted within the 10-m×30-m plots. Field sampling was conducted from June 25 to August 16, 2001.

3.2. Analytical analysis

Species cover values were used in cluster analyses to separately agglomerate in a hierarchical and nonoverlapping manner the unburned and burned vegetation relevé data. Clustering was based on squared Euclidean distance and Ward's method algorithms. The resulting dendrograms were used to identify plots with similar characteristics. Mean cover values by species were calculated for each preliminary vegetation group. Significant differences among groups were identified using Kruskal–Wallis tests (Sokal and Rohlf, 1981, pp. 429–432), because the included species were not considered to have normal distributions based on skewness (acceptable range ± 0.9) and kurtosis (-0.4 – $+1.8$) values (Wetherill, 1981). Where species percent cover differed significantly among groups, further evaluations with nonparametric Scheffé rank tests ($\propto 0.05$) were undertaken to identify where differences occurred (Miller, 1966, pp. 166-formula 110). Mann–Whitney U-tests were used for pair-wise comparisons (Sokal and Rohlf, 1981, pp. 432–433). Cluster analysis and nonparametric tests were performed with SPSS version 11.0 software. Scheffé rank tests were calculated manually.

3.3. Forage assessment

Seasonal elk forage preference index (FPI) values were calculated to provide a biologically meaningful indicator that represented the general suitability of vegetation-types. Seasonal FPI values for each sample plot were determined by weighting species cover values (C_i) by a seasonal preference rating (R_i), then dividing the sum by the total amount of plant cover (i.e. $\mathrm{FPI}=\sum C_iR_i/\sum C_i$; $i=1$, number of assessed species). Seasonal foraging preference ratings (Kufeld, 1973) were based on an ordinal scale of 0–3 scale (0-nonuse, 1-low, 2-moderate, 3-high). Species lists presented by Cook (2002) and to a lesser extent Kufeld (1973) were the primary sources of these ratings. Plants not listed in these studies were omitted from the analysis, and some modifications were made to selected species. Fall use of rough fescue (*Festuca campestris* Rydb.) and summer use of willow (*Salix* spp.) were changed from 2.5 to 3.0 and 1.7 to 3.0, respectively, based on work by Morgantini and Hudson (1989). Wildlife habitat biologists who have conducted studies along the eastern slopes of the Rocky Mountains in Alberta (B. MacCallum, University of Calgary, pers. comm.) suggested that spring and fall preferences for fireweed (*Chamerion angustifolium* (L.) Holub.) and hairy wild rye (*Leymus innovatus* (Beal) Pilger) are 2 and 0.5, respectively. These ratings were different from Cook (2002) and Kufeld (1973). In addition, bog birch (*Betula nana* L.) was downgraded from a high preference reported by Kufeld (1973) and Cook (2002) to nonuse, because regional information suggested this plant is not foraged on by elk in Alberta (MacCallum and Eslinger, 1994). Of the 113 species recorded in the study, 13 (11%) were omitted from FPI calculations because a preference rating was not available. Nine of 13 species had mean cover values of $<0.2\%$ and four had $<2\%$ cover among the different vegetation-types. FPI values of ≤ 1 (low), >1 (moderate), and >2 (high) were considered to represent different levels of forage quality. Relative changes in forage suitability (ΔFI) were assessed by weighting herbaceous biomass (kg/ha) according to FPI values.

4. Results

4.1. Unburned plant communities

Six vegetation-types were recognized within a cluster analysis dendrogram of 144 mature stands. These vegetation-types included semi-closed (2) and open-canopied (1) coniferous forest types (Table 1). Engelmann Spruce/Feathermoss forests (226 km^2) were more prevalent than Lodgepole Pine/Buffaloberry forests (38 km^2). The Engelmann Spruce/Feathermoss type had a limited herbaceous component, with graminoids and forbs having a combined cover of 6%. Hairy wild rye was the most common herb. About 40% of the ground surface was covered with mosses and lichens. The Lodgepole Pine/Buffaloberry type had similar levels of tree, shrub, herb, and nonvascular cover as the Engelmann Spruce/Feathermoss type. However, shrubs such as bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.) and buffaloberry (*Shepherdia canadensis* (L.) Nutt.) occurred more consistently in the Lodgepole Pine/Buffaloberry type. The Open Lodgepole Pine/Bearberry vegetation-type was characterized by a sparse tree canopy compared to the two other forest communities (Table 1). Bearberry dominated the ground stratum (<50 cm tall) in conjunction with common (*Juniperus communis* L.) and ground juniper (*Juniperus horizontalis* Moench). Buffaloberry was moderately abundant and was highly constant in both lodgepole pine types, but infrequent in the Engelmann spruce and other communities (Table 1). Total deciduous shrub cover averaged 45% in the Open Lodgepole Pine/Bearberry type, which was significantly ($P<0.05$) greater than in the other two forest types. Nonvascular plant cover was of limited abundance (6%) in the Open Lodgepole Pine/Bearberry type.

Forest stands were most commonly associated with valley slopes. Slope gradients among the three forest types were similar, with average values ranging from 9 to 11°. Engelmann spruce stands occurred at slightly higher elevations than the lodgepole pine types. The semi-closed forest types were associated with northeast to southeast aspects, whereas the Open Lodgepole Pine/Bearberry type occurred on southeast to south aspects (Table 1). The latter sites had subxeric moisture regimes, while the closed-canopied forests had wet-subxeric and dry-submesic moisture conditions.

Three shrub-dominated vegetation-types occurred within the study area (Table 1). The Willow–Bog Birch vegetation-type was dominated by tall (1–2.5 m tall) deciduous shrubs. Willows (*Salix* spp.) were twice as abundant as bog birch, with a combined cover of 69%. Only the Open Lodgepole Pine/Bearberry and Bearberry–Hairy Wild Rye types had a similar content of deciduous shrubs. The understory vegetation contained a variety of forbs and graminoids with $>50\%$ constancy, such as hairy wild rye, rough fescue, fireweed, and wild strawberry (*Fragaria virginiana* Duchesne). Herbs were more abundant in this community than the others, except the Shrubby Cinquefoil–Wheatgrass type (Table 1). The shrubby cinquefoil–Wheatgrass type was dominated by herbs, but vascular plant cover totaled only 43%. In this vegetation-type, bog birch had greater cover than shrubby cinquefoil (*Pentaphylloides floribunda* (Pursh) A. Löve), but occurred less consistently. Wheatgrasses (probably *Elymus albicans* (Scribn. and J.G. Sm.) A. Löve [=*Agropyron dasystachyum*]–Holland and Coen, 1982) represented a small and consistent component of this vegetation (Table 1). Most vascular species had on average $<3\%$ cover in the Shrubby Cinquefoil–Wheatgrass type. The Bearberry–Hairy Wild Rye vegetation-type was dominated (16% cover) by low-growing (<15 cm tall) bearberry. Hairy wild rye and rough fescue was the most abundant and consistently occurring herb. Shrubby cinquefoil and coniferous seedlings and trees were notable components, but occurred infrequently and had limited cover. Half as much plant cover occurred in the Bearberry–Hairy Wild Rye compared to the Willow–Bog Birch type, although comparable amounts occurred in the Shrubby Cinquefoil–Wheatgrass type.

Shrub-dominated sites were most frequently located in valley bottoms, close to rivers, or on steep escarpments that marked the edge of alluvial benches. No clear separation among shrub types occurred in stand elevations, but the Shrubby Cinquefoil–Wheatgrass type tended to occupy some of the lowest topographic positions (Table 1). Shrubby Cinquefoil–Wheatgrass and Willow–Bog Birch vegetation were most commonly associated with lower gradient slopes, whereas steep southeast to south aspects were more

Table 1
Mean percent cover (standard deviation) of prominent plant species and associated site conditions in mature vegetation-types located within east-central Banff National Park

Vegetation-types							
Variables	PIEN	PICO1	PICO2	SX	PEFL	ARUV	*P*
Overstory (>2.5 m tall) (percent cover)							
Picea engelmannii Parry *ex* Engelm. (includes *P. engelmannii* × *glauca*)	**17(7)**b	*4(5)*a	2(3)ab	<1(2)a	+(+)a[a]	2(3)a	<0.001
Pinus contorta Dougl. *ex* Loud.	1(2)a	**18(6)**b	**6(5)**ab	+(+)a	0a	2(3)a	<0.001
Understory (<2.5 m tall) (percent cover)							
Arctostaphylos uva-ursi (L.) Spreng.	<1(1)a	**2(2)**ab	**35(15)**c	0a	<1(2)a	**16(6)**bc	<0.001
Betula nana L.	<1(4)ab	0ab	1(4)ab	**20(21)**b	6(17)ab	4(14)ab	<0.001
Carex spp.	+(<1)a	0a	0a	+(+)a	*2(4)*b	+(+)ab	<0.001
Chamerion angustifolium (L.) Holub.	+(+)a	+(+)ab	0a	**2(2)**b	+(1)a	+(+)a	<0.001
Elymus spp.	+(1)a	0a	0a	2(2)ab	**4(3)**b	+(2)a	<0.001
Festuca campestris Rydb.	+(+)a	0a	+(+)ab	*1(1)*ab	**2(2)**b	*1(1)*ab	<0.001
Fragaria virginiana Duchesne	+(+)a	+(<1)a	*<1(1)*a	*2(2)*a	1(2)a	+(1)a	0.003
Geum triflorum Pursh	+(+)a	0a	0a	+(<1)a	3(4)a	<1(2)a	<0.001
Juniperus communis L.	2(4)ab	+(1)ab	4(9)b	0a	0a	1(2)ab	<0.001
Leymus innovatus (Beal) Pilger	**2(2)**ab	**2(3)**ab	*2(2)*ab	**3(3)**ab	1(2)a	**4(4)**b	<0.001
Pentaphylloides floribunda (Pursh) A. Löve	0a	+(+)ab	<1(1)ab	+(+)ab	*2(30)*b	2(2)b	<0.001
Picea engelmannii Parry *ex* Engelm. (includes P. *engelmann* × *glauca*)	2(2)b	3(3)b	<1(<1)ab	+(<1)ab	0a	**1(2)**ab	<0.001
Poa spp.	0a	0a	+(+)ab	*<1(1)*ac	*2(2)*bc	+(<1)a	<0.001
Salix spp.	2(5)a	+(+)a	+(+)a	**49(39)**b	2(7)a	<1(2)a	<0.001
Shepherdia canadensis (L.) Nutt.	3(6)ab	**9(10)**b	**9(9)**b	0a	+(+)a	2(5)a	<0.001
Growth-forms (percent cover)							
Trees (<2.5 m tall)	22(9)c	24(8)c	12(9)bc	2(4)ab	+(+)a	4(7)ab	<0.001
Deciduous shrubs	7(8)a	11(5)ab	45(13)c	71(14)bc	11(4)a	24(7)c	<0.001
Coniferous shrubs	3(5)b	<1(2)ab	4(9)b	+(1)ab	+(<1)a	5(6)b	<0.001
Forbs	4(6)a	5(6)a	3(2)a	15(15)ab	15(9)b	6(5)a	<0.001
Graminoids	2(2)a	3(3)ab	5(2)ab	8(4)bc	13(6)c	6(4)ab	<0.001
Mosses	35(6)c	25(3)bc	3(7)ab	13(3)abc	3(1)a	1(2)a	<0.001
Lichens	4(31)b	2(27)ab	3(19)ab	1(27)a	+(10)ab	1(25)ab	<0.001
Site conditions							
Mean elevation (m)	1841(133)b	1800(60)ab	1805(93)ab	1866(235)ab	1754(193)a	1785(157)ab	0.006
Typical aspect (degree)	69–174	72–175	150–170	320–38	320–205	100–181	–
Mean slope (degrees)	9(7)ab	10(8)ab	11(8)ab	7(5)ab	7(7)a	13(8)b	0.003
Mean moisture regime[b]	3.7b	4.4b	3.0ab	3.8b	2.8a	2.5a	<0.001
Mean no. elk pellet groups/ha	49(75)a	56(54)a	296(184)ab	308(329)ab	939(1172)b	202(274)a	<0.001
Number of sampled sites	27	12	9	12	55	29	

Comparison of types was based on Kruskal–Wallis tests. Row values with the same letters do not differ at the $P<0.05$ level based on Scheffé nonparametric rank tests. Italic and bold species cover values have ≥50% and ≥75% constancy, respectively. PIEN, Engelmann Spruce/Feathermoss; PICO1, Lodgepole Pine/Buffaloberry; PICO2, Open Lodgepole Pine/Bearberry; SX, Willow–Bog Birch; PEFL, Shrubby Cinquefoil-Wheatgrass; ARUV, Bearberry–Hairy Wild Rye.

[a] A '+' represents values of <0.55.

[b] Based on 1–9 scale (Beckingham et al., 1996, pp. 16–12 and 16–13): 1, very xeric; 2, xeric; 3, subxeric; 4, submesic; and 5, mesic.

commonly populated by Bearberry–Hairy Wild Rye stands. Willow–Bog Birch vegetation was associated with sites that had submesic moisture regimes, but the other two shrub types occurred on xeric to subxeric sites.

Elk pellet groups were most common in the Willow–Bog Birch, Shrubby Cinquefoil–Wheatgrass, and Open Lodgepole Pine/Bearberry vegetation-types (Table 1). Deciduous shrub vegetation contained 4–18 times more pellet groups than mature coniferous forests.

4.2. Post-burn vegetation

About seven years after burning, Engelmann Spruce/-Feathermoss vegetation (2833 ha) had less tree, ground juniper, buffaloberry, willow, and nonvascular plant cover ($P \leq 0.002$) than its unburned counterpart (Mann–Whitney *U*-tests, Tables 1 and 2). However, burned stands had increased forb (0.7X) and graminoid (5.5X) cover (P 0.001), and a greater percentage of bare ground (10% versus 1%) than unburned stands ($P < 0.001$). Hairy wild rye was the most abundant forage species in the burned Engelmann Spruce/Feathermoss vegetation-type (Table 2), with vascular plant cover totaling 23%. Similar and significant ($P <$ 0.050) changes to growth-forms occurred in burned Lodgepole Pine/Buffaloberry (795 ha). The proportion of bare ground increased from 2 to 8% (P 0.032) in the burned Lodgepole Pine/Buffaloberry stands and forb cover almost doubled (0.8X) (P 0.025). After burning, fireweed increased in abundance and was the most common species on Lodgepole Pine/Buffaloberry sites (age 6.8 years), whereas bearberry and buffaloberry abundance decreased (cf. Tables 1 and 2). In burned Open Lodgepole Pine/Bearberry stands (228 ha), the abundance of most growth-forms remained similar to their unburned composition. Exceptions included a decrease in tree cover and small increases in forb cover (cf. Tables 1 and 2).

Burned Engelmann Spruce/Feathermoss sites tended to have slightly drier moisture regimes ($P < 0.003$) and occupied a greater proportion of west to north aspects than the unburned stands, but had similar elevations and slope gradients. Burned Lodgepole Pine/Buffaloberry sites were also associated with slightly drier soil conditions ($P <$ 0.001), while occurring at higher elevations (P 0.039) and on broader range of aspects than the unburned counterpart (cf. Tables 1 and 2). No identifiable site differences were found between unburned and burned Open Lodgepole Pine/Bearberry vegetation stands.

Willow–Bog Birch communities (767 ha) experienced significant decreases in tall (1–2.5 m) willow (P 0.023) and bog birch (P 0.040) cover. Both shrub species were dominant components in the three and eight-year-old post-burn vegetation (Table 2). No substantial changes occurred in the abundance of plants within burned Cinquefoil–Wheatgrass stands (159 ha) in response to burning. Rough fescue cover increased the most within this vegetation ($P <$ 0.001, cf. Tables 1 and 2). Within the Bearberry–Hairy Wild Rye vegetation-type (118 ha), tree (P 0.048) and bearberry (P 0.007) cover decreased after burning.

Among the burned shrub types, Shrubby Cinquefoil–Wheatgrass vegetation tended to occupy lower elevational sites than the other two types. Shrubby Cinquefoil–Wheatgrass and Willow–Bog Birch types occurred on westerly and northerly aspects, respectively, with moderate slopes compared to Bearberry–Hairy Wild Rye vegetation, which occupied steep southeasterly aspects. Submesic moisture conditions were associated with Willow–Bog Birch vegetation, but xeric to subxeric regimes occurred with the other two shrub communities. Recently, burned Willow–Bog Birch stands (3 years old) occurred more commonly on easterly to southeasterly aspects as opposed to northerly aspects (P 0.017). Older (8 years) Willow–Bog Birch vegetation was present on similar aspects as younger stands, but did not have different (P 0.064) slope gradients when compared with unburned stands. The older stands and their unburned counterparts also did not differ with respect to elevations and moisture regimes. Burned Shrubby Cinquefoil–Wheatgrass vegetation occurred more commonly on easterly as opposed to westerly aspects at higher elevations (P 0.001) with slightly wetter moisture regimes than unburned stands ($P < 0.001$). Steeper slopes (P 0.043) and slight drier site conditions ($P < 0.001$) were associated with burned compared to unburned Bearberry–Hairy Wild Rye vegetation sites. Among burned shrub types, elk used Shrubby Cinquefoil–Wheatgrass vegetation most and Willow–Bog Birch (3 years) vegetation the least based on pellet group counts. Elk use increased three-fold in burned Engelmann spruce vegetation ($P < 0.001$), but remained similar to unburned levels in other types (Tables 1 and 2).

4.3. Forage biomass and preference index

Average graminoid content in unburned plant communities ranged from 76 to 481 kg/ha, with the Engelmann Spruce/Feathermoss vegetation-type having the smallest quantity (Table 3). Herb biomass was greatest in Willow–Bog Birch and Shrubby Cinquefoil–Wheatgrass stands. More than 2000 kg/ha of shrub biomass occurred in the Open Lodgepole Pine/Bearberry and Bearberry–Hairy Wild Rye vegetation-types before treatment, whereas less than 700 kg/ha was typically present in the other plant communities. Burning resulted in a significant increase in the quantity of one or more forage component in each vegetation-type (Table 3). Browse availability consistently increased in deciduous shrub communities after burning, whereas herb abundance increased dramatically in formerly tree-dominated sites. Graminoid biomass more than doubled in burned Engelmann spruce and lodgepole pine stands, but increased least (e.g. 50–150%) in the open forest and shrub-dominated vegetation-types (Table 3). Among mixed shrub–herb communities the herbaceous component increased from 336–747 kg/ha to 517–1104 kg/ha in response to burning ($P < 0.025$-Mann–Whitney *U*-test).

Table 2
Mean percent cover (standard deviation) of prominent plant species in recently burned vegetation-types located within east-central Banff National Park

Vegetation-types								
Variables	Pien	Pico1	Pico2	Sx1	Sx2	Pefl	Aruv	*P*
Plant species <2.5 m tall (percent cover)								
Achillea millefolium L.	+(+)a[a]	+(+)a	*+(+)*ab	*+(+)*ab	*<1(<1)*ab	**<1(<1)**b	+(<1)ab	<0.001
Arctostaphylos uva-ursi (L.) Spreng.	1(2)a	0a	**50(16)**b	<1(2)a	+(+)a	<1(2)a	**10(4)**b	<0.001
Betula nana L.	+(+)ab	+(+)ab	0a	**7(2)**bc	**13(9)**c	<1(2)abc	0a	<0.001
Carex spp.	+(1)a	+(+)a	0a	<1(1)a	*1(1)*a	1(1)a	<1(2)a	0.001
Chamerion angustifolium (L.) Holub.	**2(3)**ab	**6(4)**b	0a	**2(2)**ab	*<1(<1)*ab	+(<1)a	+(1)a	<0.001
Elymus spp.	+(<1)a	+(+)a	0a	+(1)a	<1(2)a	*2(3)*	+(+)a	<0.001
Festuca campestris Rydb.	<1(1)ab	+(<1)a	+(+)ab	**1(1)**ab	**3(3)**ab	**6(6)**b	*2(2)*ab	<0.001
Fragaria virginiana Duchesne	+(2)a	+(+)a	**2(2)**a	**1(2)**a	*<1(1)*a	*2(2)*a	<1(1)a	<0.001
Geum triflorum Pursh	+(+)a	0a	0a	0a	+(+)a	*3(4)*a	<1(+)a	<0.001
Hedysarum alpinum L.	+(<1)a	+(+)a	0a	+(<1)a	+(+)a	+(1)a	*+(+)*a	0.156
Hedysarum sulphurescens Rydb.	+(<1)a	0a	*<1(<1)*a	+(<1)a	0a	+(+)a	<1(1)a	0.002
Leymus innovatus (Beal) Pilger	**10(5)**b	**3(2)**a	*6(6)*ab	**4(2)**a	**3(2)**a	*2(2)*a	**5(3)**a	<0.001
Oxtropis campestris (L.) DC.	+(<1)b	+(+)b	0ab	+(+)ab	0ab	*1(2)*b	<1(1)ab	<0.001
Pentaphylloides floribunda (Pursh) A. Löve	+(+)ab	0a	+(+)ab	**1(1)**ab	**1(2)**ab	**2(2)**b	1(2)b	<0.001
Picea engelmannii Parry *ex* Engelm.	+(+)a	+(+)a	0a	0a	0a	0a	0a	0.013
Pinus contorta Dougl. *ex* Loud.	+(<1)a	1(2)a	+(+)a	0a	0a	0a	+(<1)a	0.013
Salix spp.	+(<1)a	1(2)a	0a	**21(5)**b	*6(5)*ab	+(1)a	0a	<0.001
Shepherdia canadensis (L.) Nutt.	+(<1)a	+(<1)a	**2(2)**a	0a	0a	0a	+(<1)a	<0.001
Solidago multiradiata Ait.	+(<1)a	+(+)a	0a	*1(1)*a	**1(<1)**a	+(1)a	+(+)a	<0.001
Growth-forms (percent cover)								
Deciduous shrubs/trees	2(3)a	1(2)a	52(15)b	30(6)c	21(6)b	4(3)ab	13(4)b	<0.001
Coniferous shrubs/trees	<1(1)a	1(3)a	<1(+)a	0a	0a	+(<1)a	2(5)a	0.044
Forbs	7(5)a	10(6)a	6(<1)a	10(4)a	6(4)a	15(6)ab	7(3)a	<0.001
Graminoids	13(5)bc	4(2)a	9(4)ab	7(2)abc	9(4)ab	16(8)b	8(5)abc	<0.001
Mosses	7(10)b	15(19)b	+(+)ab	3(9)ab	+(+)ab	+(<1)a	<1(3)ab	<0.001
Lichens	+(+)a	+(<1)a	0a	0a	0a	+(+)a	1(3)a	0.033
Site conditions								
Mean elevation (m)	1841(123)a	1861(99)a	1783(22)a	1853(32)a	1839(71)a	1874(108)a	1824(92)a	0.390
Typical aspect (degree)	60–135 201–348	78–232	150–186	99–149	131–160	121–180	147–173	–
Mean slope (degrees)	12(8)bc	14(8)abc	7(7)abc	3(3)a	3(1)ab	10(9)abc	18(6)c	<0.001
Mean moisture regime	3.4b	3.7ab	3.4ab	4.1b	3.3ab	3.1ab	2.4a	<0.001
Mean no. Elk pellet groups/ha	200(209)a	128(131)ab	413(252)ab	137(107)ab	281(125)ab	560(640)b	221(284)ab	0.001
Mean age (years)	6.6(4.0)c	6.8(4.0)ac	10.0(0)abc	2.9(2.7)ab	7.7(3.9)a	4.5(3.8)ab	7.7(3.7)ab	<0.001
Number of samples	47	30	5	9	7	19	14	

Comparison of types was based on Kruskal–Wallis tests. Row values with the same letters do not differ at the $P<0.05$ level based on Scheffé nonparametric rank tests. Italicised and bold values have ≥50 and ≥75% constancy, respectively. Pien, Burned Engelmann Spruce/Feathermoss; Pico1, Burned Lodgepole Pine/Buffaloberry; Pico2, Burned Open Lodgepole Pine/Bearberry; Sx1, Burned Willow–Bog Birch (3 yrs); Sx2, Burned Willow–Bog Birch (8 yrs); Pefl, Burned Shrubby Cinquefoil-Wheatgrass; Aruv, Burned Bearberry–Hair Wild Rye.

[a] A '+' represents values of <0.55.

Table 3
Changes in available forage biomass (dry weight) in response to prescribed burning within east-central Banff National Park

Growth-form	Graminoids			Forbs			Shrubs		
Vegetation-type (Mean age of burned stands)	Unburned (kg/ha)	Burn Effect (kg/ha)	*P*	Unburned (kg/ha)	Burn Effect (kg/ha)	*P*	Unburned (kg/ha)	Burn Effect (kg/ha)	*P*
Engelmann Spruce/Feathermoss (7 yrs)	76a	+567	<0.001	80a	+99	0.002	332a	−131	0.240
Lodgepole Pine/Buffaloberry (7 yrs)	88a	+200	0.112	48a	+423	<0.001	205a	−57	0.368
Open Lodgepole Pine/Bearberry (10 yrs)	99a	+78	0.028	68ab	+79	0.028	4902b	+291	0.386
Willow–Bog Birch (3 yrs)	235ab	+341	0.021	224ab	+98	0.337	653ab	+1613	0.001
Willow–Bog Birch (8 yrs)	235ab	+114	0.205	224ab	−69	0.673	653ab	+1442	0.003
Shrubby Cinquefoil-Wheatgrass (4 yrs)	481b	+255	0.024	266b	+102	0.390	194a	+150	<0.001
Bearberry–Hairy Wild Rye (8 yrs)	178a	+198	0.009	158ab	−17	0.669	2171b	−940	0.074
P	<0.001			<0.001			<0.001		

Pair-wise comparisons based on Mann–Whitney *U*-tests, whereas comparisons among vegetation-types was based on Kruskal–Wallis tests. Vegetation-types with the same letters within a growth-form do not differ ($P \leq 0.05$ level) based on nonparametric Scheffé rank tests. See Tables 1 and 2 for associated sample sizes.

The unburned vegetation-types had low to moderate elk FPI values (typically <1.2 on a 3.0 scale) (Table 4). Deciduous shrub vegetation consistently had higher index values than coniferous communities. Coniferous forest stands were particularly poor in spring (Table 4). Burning had the greatest effect on FPI values in coniferous forest stands. In these stands, index values increased almost one unit for the spring and summer seasons. Burning did not substantially affect fall FPI values. Significant increases in FPI index values among seasons and non-forest vegetation-types were limited to <0.3 units (Table 4).

5. Discussion

The recognized vegetation-types were similar to plant communities described by Holland and Coen (1982) as part of the biophysical inventory of Banff and Jasper National Parks. The Engelmann Spruce/Feathermoss type most closely approximated the composition of the *Picea engelmannii/Elymus* [=*Leymus*] *innovatus* (C33) community. The Lodgepole Pine/Buffaloberry type appeared to be either a combination or an intermediate form of the *Pinus contorta/Shepherdia canadensis/Aster conspicuus* (C6) and *Pinus contorta/Shepherdia canadensis/Linnaea borealis* (C19) types. The primary difference between these two latter types was the dominant herb in the understory. The Holland and Coen (1982) open variant of the *Pinus contorta/Juniperus communis/Arctostaphylos uva-ursi* type (C3) was very similar in composition to the Open Lodgepole Pine/Bearberry type. Stands of the Willow–Bog Birch type appeared to closely match the composition of the *Salix* spp.-*Betula glandulosa* [=*nana*]/*Erigeron peregrinus* type (S4) that was previously described in Banff National Park. The Shrubby Cinquefoil–Wheatgrass type had similarities to the *Potentilla fruticosa* [=*Pentaphylloides floribunda*]/*Arctostaphylos uva-ursi-Galium boreale* (S4) vegetation, but no equivalent was described by Holland and Coen (1982) of the Bearberry–Hairy Wild Rye type. However, examples of the Bearberry–Hairy Wild Rye type have been described elsewhere within the Subalpine zone of Alberta by Archibald et al. (1996-SA e1.6), Beckingham et al. (1996-SA a1.1), and others. From an areal perspective, the Engelmann Spruce/Feathermoss and Lodgepole Pine/Buffaloberry vegetation-types are both common in the study area and appear to be widespread throughout the Subalpine zone within the Rocky Mountains of Alberta.

Table 4
Average elk forage preference index values and net change by vegetation-type following prescribed burning in east-central Banff National Park

Season	Spring			Summer			Fall		
Vegetation-type (Mean age of burned stands)	Unburned	Burn Effect	*P*	Unburned	Burn Effect	*P*	Unburned	Burn Effect	*P*
Engelmann Spruce/Feathermoss (7 yrs)	0.58a	+0.96	<0.001	0.71a	+0.93	<0.001	0.70a	−0.21	0.010
Lodgepole Pine/Buffaloberry (7 yrs)	0.59a	+0.96	<0.001	0.79ab	+0.89	<0.001	0.92ab	−0.17	0.070
Open Lodgepole Pine/Bearberry (10 yrs)	0.75ab	+0.26	0.014	0.35a	+0.04	0.549	1.39b	−0.01	0.947
Willow–Bog Birch (3 yrs)	1.21b	+0.26	0.102	1.20b	+0.18	0.155	1.20ab	+0.18	0.522
Willow–Bog Birch (8 yrs)	1.21b	−0.27	0.151	1.20b	−0.29	0.128	1.20ab	−0.38	0.205
Shrubby Cinquefoil-Wheatgrass (4 yrs)	0.79ab	+0.25	0.002	1.18b	−0.02	0.599	0.78a	+0.19	0.811
Bearberry–Hairy Wild Rye (8 yrs)	0.81ab	+0.24	0.012	0.49a	+0.29	0.006	1.01ab	+0.03	0.816
P	<0.001			<0.001			<0.001		

Pair-wise comparisons by Mann–Whitney *U*-tests, whereas comparisons among vegetation-types was based on Kruskal–Wallis tests. Vegetation-types with the same letters within a season do not differ ($P \leq 0.05$ level) based on nonparametric Scheffé rank tests. See Tables 1 and 2 for associated sample sizes.

Some differences in site conditions were evident between unburned and burned vegetation stands, except the Open Lodgepole Pine/Bearberry type. It is thought that soil moisture availability during the growing season mostly determined the vegetation-type that occurred on a site. For example, herb and shrub community occurrences are largely a response to specific edaphic conditions (e.g. Bearberry–Hairy Wild Rye-steep southfacing slopes); therefore, differences in other site variables may not be critical to determining their presence in the landscape. In contrast, differences in moisture regimes between unburned and burned Lodgepole Pine/Buffaloberry sites appear to reflect a shift toward topographically drier sites with increasing elevation. At higher elevations, evapotranspiration demands on plants would be less due to cooler temperatures, reduced surface evaporation, and greater precipitation; making the differences in site conditions physiologically similar and ecologically less important. Moisture regimes among unburned and burned Engelmann Spruce/Feathermoss and Lodgepole Pine/Buffaloberry sites were within the ranges reported for the vegetation (Archibald et al., 1996). Although statistical differences in some site variables were evident between pairs of unburned and burned vegetation-types, these differences probably did not have major ecological effects on post-fire community development or the availability of forage.

Prescribed burning killed or severely damaged woody plants and substantially reduced the nonvascular components. Burning coniferous forests returned the vegetation to an early stage of secondary successional development, where herbs and low-growing shrubs dominated. These changes produced a >4-fold enhancement of forage abundance and increased quality (ΔFI = 1070). Seven years after burning, coniferous trees had <2% cover (Table 2), therefore, we infer that herb-dominate vegetation could persist on burned forest sites for another 20 years. Lodgepole pine re-establish more quickly than Engelmann spruce, as pine seeds survive fire in woody serotinous cones (Lotan and Critchfield, 1990). Engelmann spruce do not have similar fire adaptations, suggesting burned Engelmann spruce sites may retain a predominantly herbaceous vegetation cover longer than lodgepole pine sites, assuming they are not colonized by lodgepole pine.

Burning mixed shrub and herb vegetation did not result in the same degree of forage suitability change (e.g. ΔFI Willow–Bog Birch vegetation at three years = 606, ΔFI at eight years = 41) that occurred with coniferous stands. Many of the plants that regenerated in this vegetation-type have rhizomes or other similar asexual propagation mechanisms (e.g. bog birch, willows, hair wild rye, fireweed) that allowed them to quickly re-establish after disturbance. While herbaceous biomass on burned coniferous forest sites increased 450% above pre-burn conditions, the herbaceous biomass on mixed shrub and herb sites at best doubled and FPI values were either unchanged or increased only slightly (Tables 3 and 4). However, the proportion of shrub biomass in the mixed shrub and herb communities substantially increased. This was largely due to resprouting of shoots rather than invasion and establishment of new plants. The importance of post-burn shrub biomass increases in the Willow–Bog Birch vegetation-type (Table 3) may be exaggerated, because the totals include bog birch, which is not browsed by elk in Alberta (MacCallum and Eslinger, 1994). Based on foliar cover, bog birch may represent up to 15% and 50% of shrub biomass in the three- and eight-year-old categories of the Willow–Bog Birch vegetation-types, respectively.

Potential fire-induced changes in elk carrying capacity were estimated based on two vegetation growing season scenarios (May, and May through August). Current research in the study area (M. Hebblewhite, University of Alberta, pers. comm.) indicates that elk use the Subalpine zone in the spring before green-up in the higher elevation Alpine zone, i.e. 30 days (scenario 1). Alternatively, elk may remain in burned areas in the Subalpine zone throughout spring and summer, i.e. 120 days (scenario 2). Scenario models were based on the assumptions that: (i) elk consume 6.6 kg of forage per day (Watkins et al., 1991); (ii) 80% of the forage is herbaceous material (Morgantini and Hudson, 1989; Cook, 2002; Tiedemann and Woodard, 2002); (iii) the recommended proper use factor (grazing intensity) for forage in spring is 10% of peak biomass, and for the entire summer it is 25%; and (iv) the six recognized vegetation-types comprised about 94% of the prescribed burn area (5223 ha; see results). Under scenario 1, the area would sustain grazing by 694 elk in the absence of burning, or 2328 elk after treatment. Under scenario 2, unburned vegetation could support grazing by 433 animals or 1455 elk after burning, 73% of the potential enhancement is contributed by Engelmann Spruce/Feathermoss sites. The enhanced carrying capacity under scenario 2 is the equivalent of 28 elk per 100 km^2, which is a relatively high density for secondary elk range (i.e. 1–20 animals/ha-Stelfox and Stelfox, 1993). More refined estimates of carrying capacity could be based on nutritional parameter, because biomass alone can result in the overestimation of carrying capacity (Hobbs and Swift, 1985). The increase in elk pellet group density in burning areas, however, is consistent with the expected increased quality and observed increase in forage presence after burning (cf. Tables 1 and 2).

Realization of the habitat enhancement potential from prescribed burning in the study area may be constrained by several factors. For example, none of the sampled vegetation-types were high quality elk foraging areas after burning. Further, other ungulate species could compete for forage in burned sites reducing forage for elk. Phenology is also an important factor (Gates and Hudson, 1981; Peck and Peek, 1991; Cook, 2002); the protein content of summer forage declines rapidly after mid-summer (Morgantini and Hudson, 1989). Other studies have found important, but often short-lived improvements in forage quality, as measured by crude protein, digestibility, and nutrient content of forage plants following burning (Daubenmire, 1968; Leege and Hickey, 1971; Hobbs and Spowart, 1984; Weber et al., 1984; Wambolt et al., 2001). Also, the quality of forest understory herbs may decrease when growing in open environments (East and Felker, 1993). Finally, predation may strongly influence elk density in many areas of the Canadian Rocky Mountains (Hebblewhite et al., 2002). Each of these factors could limit the effectiveness of elk habitat enhancement by prescribed burning. In addition to elk, other large mammals may benefit from prescribed burning, including bighorn sheep (Smith et al., 1999) and grizzly bears (Hamer, 1999). However, habitat management for these or other wildlife species should be considered in the context of historic patterns of landscape and biological diversity.

6. Conclusions

Prescribed burning of coniferous Subalpine forests substantially increased forage availability, and resulted in the greater abundance of herbaceous plant species that are more preferable to elk, with the effect of the treatment lasting at least a decade. In contrast, burning of mixed deciduous shrub and herbaceous vegetation reduced the total cover of tall woody plants, but resulted in minimal or only a short-term increase in herbaceous biomass, although browse production as a result of resprouting was stimulated.

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